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A consistent hierarchy in the fungal feeding preferences of the Collembola *Onychiurus armatus*

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1. Introduction

Collembola have been thought to be generalist feeders, on the basis of the wide variety of potential foodstuffs present in the guts of field collected animals (BÖDVARSSON 1970, ANDERSON & HEALEY 1972, KILBERTUS & VANNIER 1979). However, when Collembola are presented with a limited choice of food in a controlled environment, several authors have noted that clear preferences are shown (SINGH 1969, McMILLAN 1976, VISSER & WHITTAKER 1977). A solution to this paradox is suggested by the results of KNIGHT & ANGEL (1967), who found that although fungal spores were the preferred food to *Tomocerus flavescens* in the laboratory, they were not a dominant item in the guts of animals in the field. These results suggested that the lack of specialization in the field was a consequence of the low availability of the preferred food.

The factors determining the palatability of a foodtype to a collembolan are not known, but some factors have been suggested to influence attractiveness. MILLS & SINHA (1971) noted that *Hypogastrura tullbergi* preferred fungi which formed low mats, over which the animals could walk. BOOTH (1980) found that the palatability of *Hypholoma fasciculare* to *Folsomia candida* increased with the nitrogen level of the fungal culture medium, but that this relationship was parabolic for the more preferred fungus *Coriolus versicolor*, where palatability peaked at medium nitrogen levels. On the basis of preliminary results from dichotomous feeding experiments, SHAW (1985) proposed that *Onychiurus armatus* avoids feeding on fungi containing toxic secondary metabolites.

Two sets of authors have investigated the interactions between Collembola of the genus *Onychiurus* and saprophytic soil fungi, both using feeding preference tests followed by microcosm experiments (VISSER & WHITTAKER 1977, NEWELL 1984a). In both cases it was found that there was a marked preference for certain of the fungi, and that in a microcosm situation the competitive ability of the preferred fungus was selectively reduced by the presence of Collembola (PARKINSON, VISSER & WHITTAKER 1977, 1979; NEWELL 1984b). These results show that it may be valid to extrapolate from laboratory feeding experiments to infer grazing behaviour in the soil, although the results of KNIGHT & ANGEL (1967) show that preferred food sources may not always be available in the field.

There are two reasons to be cautious about the use of cultured fungi in feeding choice experiments. Firstly there is the problem that hyphae of a long-established fungal isolate may exhibit different chemical characteristics to hyphae growing in soil (FOSTER 1949). Secondly, LEONARD (1984) showed that the order of preference shown by *Folsomia candida* for three species of saprophytic fungi depended on the nature of the fungal culture medium. In the light of LEONARD's results, it is important that any series of choice experiments includes some attempt to test the stability of the results, either by using a range of culture media or by including an additional estimate of food quality (e.g. fecundity, moulting or mortality rates on a given fungal diet).

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Previous workers using microarthropods in choice experiments have often presented the animals with the entire spectrum of food types simultaneously (SINGH 1969, McMILLAN 1976, SAICHUE, GERSON & HENIS 1972, LEONARD 1984). This method has the weakness that Collembola tend to aggregate (JOOSSE, VERHOEF & NAGELKERKE 1977) so that the majority of animals occur on the most favoured food, giving an excessively low estimate of the palatability of the remaining foods. It could also give erratic or inconclusive results if the preferences follow a complex (non-linear) hierarchy (APPLEBY 1985). VISSER & WHITTAKER (1977) used dichotomous choices, but did not report testing all available combinations of fungi, so that the possibility of a complex hierarchy cannot be ruled out.

The aim of the experiments described below was to discover the relative palatabilities of twelve species of woodland fungi to the Collembola *Onychiurus armatus*, and to investigate whether the hierarchy was linear or complex. All experiments used fungi grown on the same nutrient agar; as a test of the reliability of the preferences discovered, populations of Collembola were constrained to a single fungus diet (using four representative fungi) to discover the rates of mortality, egg production and moulting.

2. Materials and methods

2.1. Species

All experiments described here used the collembolan *Onychiurus armatus* (TULLBERG 1869) s. lat. [Fjellberg 1982], referable to *O. aurantiacus sensu* PITKIN (PITKIN 1980). The insects came from litter collected under stands of Lodgepole pine (*Pinus contorta*) (DOUGL. ex LOUD.) in Spadeadam forest, Northumberland (National Grid Reference NY 620 740) during 1983 and 1984. The litter was stored in large plastic bags at 5 °C until the arthropods were extracted in a large Tullgren funnel. Specimens of *O. armatus* were separated and kept in single species culture in plastic boxes floored with a 10: 1 plaster of paris: charcoal mixture (GOTO 1960). These cultures were stored at 5 °C and fed with brewer's yeast.

The fungi used were a mixture of mycorrhizal and saprotrophic species. Unless otherwise stated, isolates came from culture collections maintained at ITE Merlewood, and ITE culture codes are given. The saprotrophs were *Clitocybe* sp. (isolated from spores from Spadeadam forest 1983), *Marasmius androsaceus* M9192, *Mycena epipterygia* M9228 and *Mycena galopus* M9430. The mycorrhizal species were *Hebeloma crustuliniforme* HC001, *Laccaria proxima* LP4, *Lactarius rufus* LR83 (isolated from cap tissue from Spadeadam 1983), *Paxillus involutus* PI16, *Pisolithus tinctorius* 008 (Sheffield University culture collection), *Rhizopogon roseolus* FC0032, *Suillus bovinus* 069 (Sheffield University culture collection) and *Suillus luteus* SI001.

2.2. Experimental procedures

All choice experiments were performed in choice chambers consisting of 5 cm diameter transparent plastic pill boxes, floored with a depth of approximately 0.4 cm of the 10: 1 plaster of paris: charcoal mixture, into which had been sunk three 0.9 cm diameter holes. The fungi were grown on Oelbe 02 agar (after J. DIGHTON). This nutrient medium is composed as follows (in g per litre of distilled water): L. Asparagine (2.5), KH_2PO_4 (7.0), Na_2HPO_4 (3.0), NaCl (1.0), $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ (1.0), Yeast extract (1.0), Glucose (20.0), Agar agar (12.0).

The medium was autoclaved at 138 kPa (20 psi) for 15 minutes.

The experiments involved 0.8 cm diameter cylinders of agar, aseptically removed with a cork borer from the growing edge of a colony (VISSER & WHITTAKER 1977). These agar cylinders were fitted into holes in the choice chambers floor so as to be flush with the surface, so that the Collembola had ready access to the mycelial surface.

At the start of each choice experiment, each choice chamber was fitted with discs from the two fungi under comparison and a third disc of sterile Oelbe 02 agar. Approximately 20 Collembola were pooted in, having been starved for 24 hours previously. The number of animals apparently feeding on each disc was recorded up to three times daily (at intervals of not less than four hours), and the experiment was terminated after five days or when the discs became unsuitable (due to contamination, desiccation, etc.). At the end of each experiment the number of animals surviving was counted, the percentage area eaten was estimated for each agar disc, and the number of faecal pellets on the upper surface of each disc counted using a zoom ($\times 7$ to $\times 30$) binocular microscope. Every comparison between fungi was replicated at least three times. Between experiments, choice chambers were scrubbed out using 90% ethanol to curtail the growth of contaminatory microorganisms.

The diet suitability experiments were run with the same 5 cm diameter pill boxes as the choice experiments, except that a 10 mm² coverslip was sunk into the plaster in the centre of each chamber. The coverslip acted to prevent nutrients leaching from the agar into the plaster. Each chamber held

20 specimens of *O. armatus* and one fungal disc, the disc sitting on the coverslip and being replaced at weekly intervals. The diets supplied were *L. rufus*, *Ma. androsaceus*, *My. galopus*, *H. crustuliniforme*, and a control diet of sterile Oelbe 02 agar. There were six replicates of each diet.

Chambers were examined approximately daily throughout the 14 weeks of the experiment; a total of 66 observations were made. Each examination consisted of scanning the chamber under a $\times 10$ binocular microscope for eggs, dead or moribund animals and exuviae, any of which were noted and removed. Dead animals were replaced by an equal number of adult animals which had previously been removed from the main cultures and kept without food for at least 24 hours. When contaminatory growth became evident in the chamber, the Collembola were transferred to a fresh container, along with their fungal disc.

2.3. Statistical methods

Each count of animals feeding was converted into a proportion of the animals present (estimated as the number of animals alive at the end of the experiment), and subjected to the arc-sin transformation (STEEL & TORRIE 1981, p. 236). These proportions were pooled for all experiments testing a given pair of fungi, and the significance of the differences calculated by a Student's *t*-test. As a test of robustness, the same data were analysed by the Kruskal-Wallis test (STEEL & TORRIE 1981, p. 544), a non-parametric test which was found to give closely similar significance levels to the *t*-test. In the diet suitability experiments, all data were transformed by $\ln(1 + x)$ and subject to 2-way analysis of variance using the GENSTAT package (Anonymous 1980).

3. Results

3.1. Choice experiments

To compare the 12 fungal isolates a total of 66 interspecific comparisons were made, of which 43 produced a statistically significant difference ($p < 0.05$). For each isolate, both the number of isolates significantly preferred to it and the number of isolates significantly less preferred than it were counted. The difference between these two figures was used as an objective palatability ranking, shown in Table 1. Using this ranking, the results from the 66 comparisons are summarised in matrix format in Table 2. It may be seen that the preferences form a hierarchy which is anomaly-free, although several results are non-significant when a significant difference would have been expected.

Although each experiment included a control disc of uninfected agar, there was no suggestion that these were ever fed upon. Collembola were only occasionally present on these discs, and never appeared to be feeding, nor were feeding marks ever noted, despite being clearly visible in the agar of many fungal discs. It was concluded that feeding activity on these discs was negligible. By contrast, both the faecal pellet counts and the estimates for area eaten showed highly significant variation between fungi ($F_{11, 534} = 27.3$ and 23.0 respectively) with means ranked in a closely similar order to the feeding hierarchy (see Table 3).

Table 1. The derivation of the palatability rankings

Fungus	Abbr.	Number of isolates "below" (signifi- cantly less preferred)	Number of isolates "above" (i.e. those significantly more preferred)	a—b	
		(a)	(b)		
<i>Lactarius rufus</i>	Lr	8	0	8	1
<i>Marasmius androsaceus</i>	Ma	9	1	8	2
<i>Laccaria proxima</i>	Lp	7	0	7	3
<i>Suillus luteus</i>	Sl	6	1	5	4
<i>Suillus bovinus</i>	Sb	4	1	3	5
<i>Mycena galopus</i>	Mg	4	4	0	6
<i>Mycena epipterygia</i>	Me	3	4	—1	7
<i>Rhigopogon roseolus</i>	Rr	1	4	—3	8
<i>Pezizillus involutus</i>	Pi	2	6	—4	9
<i>Pisolithus tinctorius</i>	Pt	0	7	—7	10
<i>Hebeloma crustuliniforme</i>	Hc	0	8	—8	11.5
<i>Clitocybe</i> sp.	Cl	0	8	—8	11.5

Table 2. A summary of the results of the feeding preference experiments, with the fungi arranged in order of decreasing palatability using the ranking shown in table 1

Y axis fungi	X axis fungi:											
	Lr	Ma	Lp	Sl	Sb	Mg	Me	Rr	Pi	Pt	He	Cl
Lr	X	>	=	=	=	>	>	>	>	>	>	>
Ma	<	X	=	>	>	>	>	>	>	>	>	>
Lp	=	=	X	=	=	>	>	>	>	>	>	>
Sl	=	<	=	X	=	>	>	=	>	>	>	>
Sb	=	<	=	=	X	=	=	=	>	>	>	>
Mg	<	<	<	<	=	X	=	>	=	=	>	>
Me	<	<	<	<	=	=	X	=	=	>	>	>
Rr	<	<	<	=	=	<	=	X	=	>	=	=
Pi	<	<	<	<	<	=	=	=	X	=	>	=
Pt	<	<	<	<	<	=	<	<	=	X	=	=
He	<	<	<	<	<	<	<	=	<	=	X	=
Cl	<	<	<	<	<	<	<	=	=	=	=	X

The symbolic abbreviations are as follows: >: Y axis fungus is significantly preferred to X axis fungus; <: Y axis fungus is avoided relative to X axis isolate; =: There is no significant preference shown between the fungi; X: The comparison was not made. The fungi are identified using the abbreviations shown in Table 1.

Table 3. Results for faecal pellet counts and disc area eaten at the end of each experiment

Fungus	Mean faecal pellet count	Mean % area eaten
<i>Marasmius androsaceus</i>	74.8a	72.2a
<i>Laccaria proxima</i>	70.8a	41.4b, c
<i>Lactarius rufus</i>	64.5a	55.7b
<i>Suillus luteus</i>	48.9a	50.7b
<i>Mycena galopus</i>	19.2b	68.2c, d
<i>Suillus bovinus</i>	16.6b, c	18.2d
<i>Rhizopogon roseolus</i>	13.8b, c	20.7d
<i>Paxillus involutus</i>	13.1b, c	21.3d
<i>Mycena epipterygia</i>	10.6c	24.2d
<i>Pisolithus tinctorius</i>	2.1d	0.2e
<i>Clitocybe</i> sp.	1.1d	1.2e
<i>Hebeloma crustuliniforme</i>	1.0d	1.7e

For faecal pellet count, $F_{11,534} = 37.3^{**}$

For % area eaten, $F_{11,534} = 23.0^{**}$

These data were transformed [by $\log(x + 1)$ and by the arc-sin transformation respectively] for analysis of variance and backtransformed for the table of means. Values followed by the same letter are not significantly different according to the Waller-Duncan t-test.

The mortality rates in these experiments were low; typically zero, and never more than 3 animals died during the course of observations. Mortality was regressed against a matrix of dummy variables (indicating presence or absence of each fungal isolate), and none of the 12 regression coefficients obtained was found to be significantly different from zero. This could mean either that none of the fungi were toxic, or that the toxic isolates were avoided.

3.2. Diet suitability experiments

The results of these experiments are summarised in Table 4, which shows there to have been significant variation between diets for the rates of exuviae production and of mortality, but not for egg production. According to the Waller-Duncan t-test (STEEL & TORRIE 1981, p. 190) the data on exuviae production splits into two distinct groups, with *H. crustuliniforme* in the same group as the unfed control (the low production group) and the other 3 fungi forming a second group. The same test detects 4 distinct levels in the mortality data, with

Table 4, part i. The treatments from the restricted diet experiments

Diet	Mean exuviae production/animal/day	Mean mortality rate animal/day	Mean egg production animal/day
Unfed Control	0.0111a	0.0172a	0.0093a
<i>H. crustuliniforme</i>	0.0109a	0.0127b	0.0158a
<i>M. galopus</i>	0.0238b	0.0101c	0.0151a
<i>M. androsaceus</i>	0.0253b	0.0067d	0.0137a
<i>L. rufus</i>	0.0252b	0.0094c	0.0263a

Means followed by the same letter are not significantly different, according to the Waller-Duncan t-test.

Table 4, part ii. The analysis of variances on data from the restricted diet experiment

Source of Variance	d. f.	F ratios due to		
		Exuviae production	Mortality rate	Egg production
diet	4	24.1**	10.0**	1.7 NS
time	65	2.5**	3.3**	1.6**
diet \times time	260	1.2 NS	1.1 NS	1.3**
residual	1,620			

L. rufus (the most preferred isolate) causing a significantly higher mortality rate than *M. androsaceus* (the second most preferred isolate).

4. Discussion

Previous authors who have used behavioural methods to investigate collembolan feeding habits, are unanimous that these insects appear to show preferences between foodstuffs (i.e. JOOSSE & VERHOEF 1982; LEONARD 1984; McMILLAN 1976; SINGH 1969; VISSER & WHITTAKER 1977). The findings presented above agree fully with this pattern. However, caution is indicated since the statistical methods used implicitly assume all observations to be independent. Since some animals might not have moved in the 4 hours between observations, and since Collembola are known to aggregate in response to pheromonal cues (JOOSSE, VERHOEF & NAGELKERKE 1977) this assumption of independence is questionable. Erroneous assumptions of statistical independence lead to spuriously high degrees of freedom, a condition termed "pseudoreplication" which permeates ecological research (HURLBERT 1984). All previous researchers on Collembola feeding preferences have used equivalent statistical methods; an extreme case being JOOSSE & VERHOEF (1982) who observed cultures of *Orchesella cincta* every 5 minutes for 3 hours then treated all observations as being independent. Ideally each "observation" should be of a separate experiment, but this tends to be prohibitively demanding of resources.

An extreme viewpoint would be that the "significant" results normally obtained from such feeding experiments are in fact random noise whose apparent significance is due to a combination of aggregation and statistical pseudoreplication. The data presented above form a perfect preference hierarchy when the fungi were ranked by an objective ranking procedure, and the chances of this occurring in genuinely random data can readily be examined by computer simulations. Table 5 lists the results of simulation runs in which values of -1 , 0 and $+1$ (corresponding to $x < y$, no significant difference, and $x > y$ respectively) were assigned to a play-off matrix of n "fungi" with the same probabilities as in the play-off matrix shown in Table 2 (43/132, 46/132 and 43/132 respectively). The fungi were then ranked using the procedure shown in Table 1, and the number of anomalies (events when a

Table 5. The results of computer simulations in which random preference hierarchies were created then ranked using the same ranking procedure as was used for the Collembola choice data (Table 1)

Number of "fungi"	Mean number of anomalies	Standard deviation of number of anomalies	Z score equivalent to zero anomalies
n	\bar{x}	σ	\bar{x}/σ
2	0	0	—
3	0.67	0.81	0.83 NS
4	1.49	1.13	1.32 NS
5	2.60	1.48	1.76 NS
6	4.03	1.74	2.32*
7	5.80	2.08	2.79**
8	7.18	2.51	3.18**
9	10.31	2.79	3.70***
10	12.98	3.14	4.13***
11	15.76	3.48	4.53***
12	19.06	3.67	5.19***
13	22.81	4.21	5.42***
14	26.60	4.49	5.92***
15	30.77	4.81	6.40***

The number of anomalous events (i.e. instances where a low ranking "fungus" was found to preferred to a higher ranking one) was recorded. The simulation was run 1,000 times for each value of n (the number of "fungi") and both mean and standard deviation of the number of anomalies recorded. The likelihood of finding zero anomalies can be estimated from the value of mean \div standard deviation.

"fungus" was found to be preferred to a higher ranked "fungus") were recorded. The simulation was run 1,000 times, using values of n from 2 to 15, giving estimates of the mean and standard deviation of the number of anomalies arising from random data. The value of (mean/standard deviation) is a good estimate of the normal deviate equivalent to zero anomalies, and becomes significantly large for $n > 5$. Hence any series of dichotomous choice tests involving 6 or more diets which yields a perfect hierarchy may be assumed to be derived from non-random data, and for the data presented above a null hypothesis that the results are artefacts of pseudoreplication may be rejected with a very high level of confidence.

Since it seems that a genuine preference hierarchy has been discovered in the choice experiments, the question arises of what factors affect the palatability of these fungi to Collembola. MILLS & SINHA (1971) stated that mycelial morphology was an important factor for *Hypogastrura tullbergi*, with low mats being preferred to dense swards. All the fungal isolates used in the experiments described above were of a similar low, mat-like growth form, so this variable is probably of little importance here. The other two factors likely to influence choice are both chemical, these are the nutrient richness of the mycelium and the extent to which it contains toxic or repulsive secondary metabolites. No chemical analyses were performed on the mycelia, so this question cannot finally be resolved, but when the edibility to humans of the fungi is included alongside the preference hierarchy it can be seen that the less palatable species to *O. armatus* are also inedible or toxic to humans (Table 6). NEWELL (1984a, b) investigated the interactions between *Marasmius androsaceus* and *Mycena galopus* in the presence and absence of *Onychiurus latus* (a member of the *O. armatus* group), and found that *My. galopus* was the slower growing of the two fungi, but was less palatable, and could out-compete *Ma. androsaceus* when both fungi were subjected to grazing pressure. This suggests that *My. galopus* was allocating a substantial proportion of its metabolic resources to herbivore deterrence, presumably by production of repellent chemicals. A similar thesis was presented by PARKINSON, VISSER & WHITTAKER (1977, 1979) who also found that selective grazing by *Onychiurus* altered the outcome of competition between fungi. WICKLOW and YOCOM (1982) found that the presence of larvae of the sciarid *Lycoriella mali* (Diptera) in rabbit dung decreased the number of species of coprophilous fungi sporulating, and increased the relative abundance of *Chaetomium* sp., a fungus that these larvae are

Table 6. The palatability to humans of the sporophores of the fungi used in the feeding preference experiments

Species	Palability
<i>Lactarius rufus</i>	edible after removal of latex ¹⁾
<i>Marasmius androsaceus</i>	edible but worthless
<i>Laccaria proxima</i>	edible
<i>Suillus luteus</i>	edible and good
<i>Suillus bovinus</i>	edible and good
<i>Mycena galopus</i>	edible but worthless
<i>Mycena epipterygia</i>	edible but worthless
<i>Rhizopogon roseolus</i>	inedible (toxic to slugs ²⁾)
<i>Pezizillus involutus</i>	dangerously toxic
<i>Pisolithus tinctorius</i>	uncertain, thought to be inedible
<i>Hebeloma crustuliniforme</i>	dangerously toxic, though not deadly
<i>Clitocybe</i> sp.	this genus varies widely in edibility

¹⁾ B. SÖDERSTRÖM pers. comm. The latex found in the sporophore was not produced in the mycelial cultures.

²⁾ S. VISSER pers. comm.

The information on edibility is taken from LANGE & HORA (1961) and PHILLIPS (1981) unless otherwise indicated. The fungi are organized into descending order of acceptability to *Onychiurus armatus*.

known to refuse as food (WICKLOW 1979). Again there is no proof as to the nature of the defensive system used by the fungus.

The results from the restricted diet experiments agree almost perfectly with the feeding preference hierarchy, with one exception. The anomaly is that the mortality rate was found to be significantly lower on a diet of *M. androsaceus* than on *L. rufus*, even though *L. rufus* was above *M. androsaceus* in the preference hierarchy. Such a discrepancy between the results of choice experiments and long-term diet experiments is not without precedent. BROADHEAD (1957) examined the preferences of nine species of psocids (Insecta: Psocoptera) for two diets, the alga *Pleurococcus viridis* and the lichen *Lecanora conazeoides*. Only two species preferred the lichen, and one of these survived better and produced more eggs when confined to the less favoured diet of algae. Broadhead interpreted this as showing its lichenivory to be a recently evolved phenomenon; this may be because *L. conazeoides* is a very pollution tolerant species, which was extremely rare before the industrial revolution but is now one of the commonest lichens in the U.K. (DOBSON 1979).

In conclusion, these experiments have shown that the preferences of *O. armatus* for 12 woodland fungi form a perfectly consistent hierarchy, and that the preference rankings broadly agree with the suitability of the fungi as a long term diet. It is not certain which factors determined the palatability of the fungi to *O. armatus*, but there was a trend for low ranking fungi to be species whose sporophores are known to be toxic to humans and other animals. This implies that the mycelia of these fungi gain some protection against grazing by production of toxic metabolites.

It is very noteworthy that three of the ectomycorrhizal fungi used were readily eaten by *O. armatus*, and that the most preferred fungus was an isolate of the common mycorrhizal symbiont *Lactarius rufus*. The widespread occurrence of grazing on extracortical mycorrhizal hyphae would have many implications both for studies on mycorrhizal function and for the understanding of energy fluxes in the soil ecosystem.

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The fungal feeding preferences of the Collembola *Onychiurus armatus* were examined by means of dichotomous choice tests. Agar-grown isolates of twelve woodland fungi were used, each isolate being tested against all the others. A perfectly consistent preference hierarchy was found, with the most highly preferred species being the mycorrhizal species *Lactarius rufus*. The suitability of each of four of the test fungi as a long term diet was examined, and found to agree closely with their preference ranking.

Key words: Collembola, mycophagy, feeding, fecundity, choice test, hierarchy, mycorrhizal fungi, grazing.